The demography of *Acacia* stands on the Hluhluwe-Umfolozi Game Reserve

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Abstract

Little is known about the demographics of the genus *Acacia* in Africa, despite its prominence and the economic and environmental importance of this group. The demographics and species composition of stands of four different *Acacia* species was investigated in the Hluhluwe-Umfolozi Game Reserve in northern Kwazulu-Natal in order to determine whether stands were self-replacing, or whether other *Acacia* species were invading them. Soil and stand density as well as the density and composition of the grass layer were investigated in order to determine whether any of these affected *Acacia* demography and species composition. In three out of four cases, the species whose large size class dominated the stand (known as the "stand species") was found to have a strongly bimodal size class distribution, skewed primarily towards the large size class and secondarily towards the small size class. Other *Acacia* species in the stands, with few or no large individuals present ("non-stand species") tended to have unimodal size class distributions, skewed primarily towards the small size class and secondarily towards the medium size class. Based on the proportion of small to large individuals, non-stand species are more likely to increase in overall numbers in future, suggesting that the species composition of the stands may be in a state of flux. Few relationships were found between stand density, grass density, grass composition and numbers of small and medium acacias. This could be as a result of differentiation between *Acacia* species, meaning that they cannot be analysed collectively. Furthermore sample sizes of individual species may have been too small to analyse individually. Alternatively it could mean that none of these factors have a significant effect on one another and that other explanations need to be found for the demographics of this genus.

Introduction

Acacia are regarded as the quintessential African tree (Midgley & Bond 2001). They are nitrogen fixers, important forage species (Gourlay 1995), and some are initiators of the process of bush encroachment in commercial and conservation areas (Skowno *et al.* 1999, Moleele *et al.* 2002). More than 100 species are distributed in savannas throughout the continent (Ross 1979). Despite being significant components of the woody stratum of these ecosystems, however, very little is known about many aspects of their ecology, including their demography. The savanna ecosystems of which they form part, a co-existence of grass and trees, are subject to a variety of factors including rainfall, fire, herbivory, and the nature of the soil (Scholes & Walker 1993).

Midgley and Bond (2001) noted that *Acacia* have many demographic hurdles to overcome on their way to becoming adults. Sufficient rainfall over a prolonged period of time is required for germination. Thereafter the impacts of fire and herbivory are significant hurdles for small plants, which are within reach of flames and browsers. These short *Acacia* are not necessarily very young. Some, termed "gullivers" by Bond and van Wilgen (1996), may have merely been prevented from growing taller by repeated burning.

Higgins and co-workers (2000) argued that the persistence of woody plants in savannas depends on the intensity of fires, with occasional periods of low fire intensity being crucial for small woody plants to escape the "fire-trap". They produced a model of the demography of overall populations of woody plants that suggests how populations fluctuate with different fire regimes. They envisage escape from fire as being the dominant process and therefore their model predicts bimodal population structures (many small/suppressed individuals and larger escaped individuals, with few intermediate sized individuals). In all populations examined in this study, the term "bimodal" refers to size class distributions where the large and small size classes were at least twice the magnitude of the medium size class.

The aim of this study was to investigate the demographics of certain stand-forming *Acacia* species that occur on the Hluhluwe-Umfolozi Game Reserve and to determine whether this demography is influenced by fire and herbivory. I asked whether *Acacia* populations in the

Reserve had a bimodal size class distribution and whether this was associated with fire dominated systems. Bond and co-workers (2001) argue that some *Acacia* species recruit under conditions of low herbivory and others under conditions of low fire. On Hluhluwe-Umfolozi they suggested that changes in the disturbance regime from a herbivore-dominated system to a fire dominated system has lead to *Acacia karroo*, a fire tolerant species, replacing *Acacia nilotica*, a less fire tolerant species that appears more herbivore adapted (Brooks & Owen-Smith 1994, Bond *et al.* 2001, Archibald & Bond 2003). I wished to establish whether these compositional changes were general among stands of different *Acacia* species on the Reserve, and whether there was any correlation between the density and composition of these stands, and the density and composition of associated grasses.

Study area

The study took place on the Hluhluwe-Umfolozi Game Reserve ($28^0$00'-$28^0$26' S, $31^0$43'-$32^0$09'E) (Fig 1) in Zululand, northern Kwazulu-Natal, South Africa. The Reserve covers an area of approximately 900km^2, with altitudes ranging from 60-750m above sea level (Whately & Porter 1983). Hluhluwe, the northern portion of the Reserve, is for the most part, at higher altitude than Umfolozi in the south. The Reserve has a summer rainfall regime, which peaks between October and March. There is a rainfall gradient, which follows the altitudinal gradient between the Hluhluwe and Umfolozi sections of the Reserve. Hluhluwe receives higher rainfall, with an average of around 990mm per year, while Umfolozi receives around 720mm per year (Whately & Porter 1983). Within the context of Zululand savanna, these are regarded as mesic and arid savanna respectively. This distinction is reflected in the nature of the veld. In the moister Hluhluwe, production (particularly of grass) is higher than Umfolozi, resulting in a greater fire fuel load, and therefore a more fire-prone environment. In the more arid and less productive Umfolozi fire plays less of a role, and it is believed that the role of large herbivores is greater in determining the dynamics of the vegetation than in Hluhluwe (Bond et al. 2001).

The veld in the Reserve is predominantly Lowveld, a sub-category of Bushveld, while most of the remainder is Zululand Thornveld (Acocks 1988). *Acacia* occur scattered or in stands of adults of fairly uniform size and species structure. Some *Acacia* species appear more prone to stand-formation than others on the Reserve. Stands of *Acacia burkei* and *A. nilotica* were sampled ~~on~~ in Hluhluwe, while stands of *Acacia nigrescens* and *Acacia tortilis* were sampled ~~on~~ in Umfolozi.

The grass layer varies between the more extensive bunch grass dominated areas, and areas where lawn-forming grasses dominate. Many, but not all of the lawn grasses are stoloniferous. Together with certain grazing-tolerant bunch grass species, the stoloniferous grasses form what have been referred to as lawn grass communities, while tall, grazing-intolerant bunch grasses form bunch grass communities (McNaughton 1984). Lawn grass communities occur as fragments in a matrix of bunch grass. They tend to exclude fire due to their minimal fuel load, and therefore fire is not a major driver of vegetation dynamics within these patches (Bond *et al.* 2001). They are however subject to more intensive grazing than bunch grass on the whole. Indeed it is this grazing that maintains the lawns. Were it not for the grazers' continual cropping of the grass before it rises above the lawn layer, bunch grass community species would invade and out-compete the lawn grass communities (McNaughton 1984).

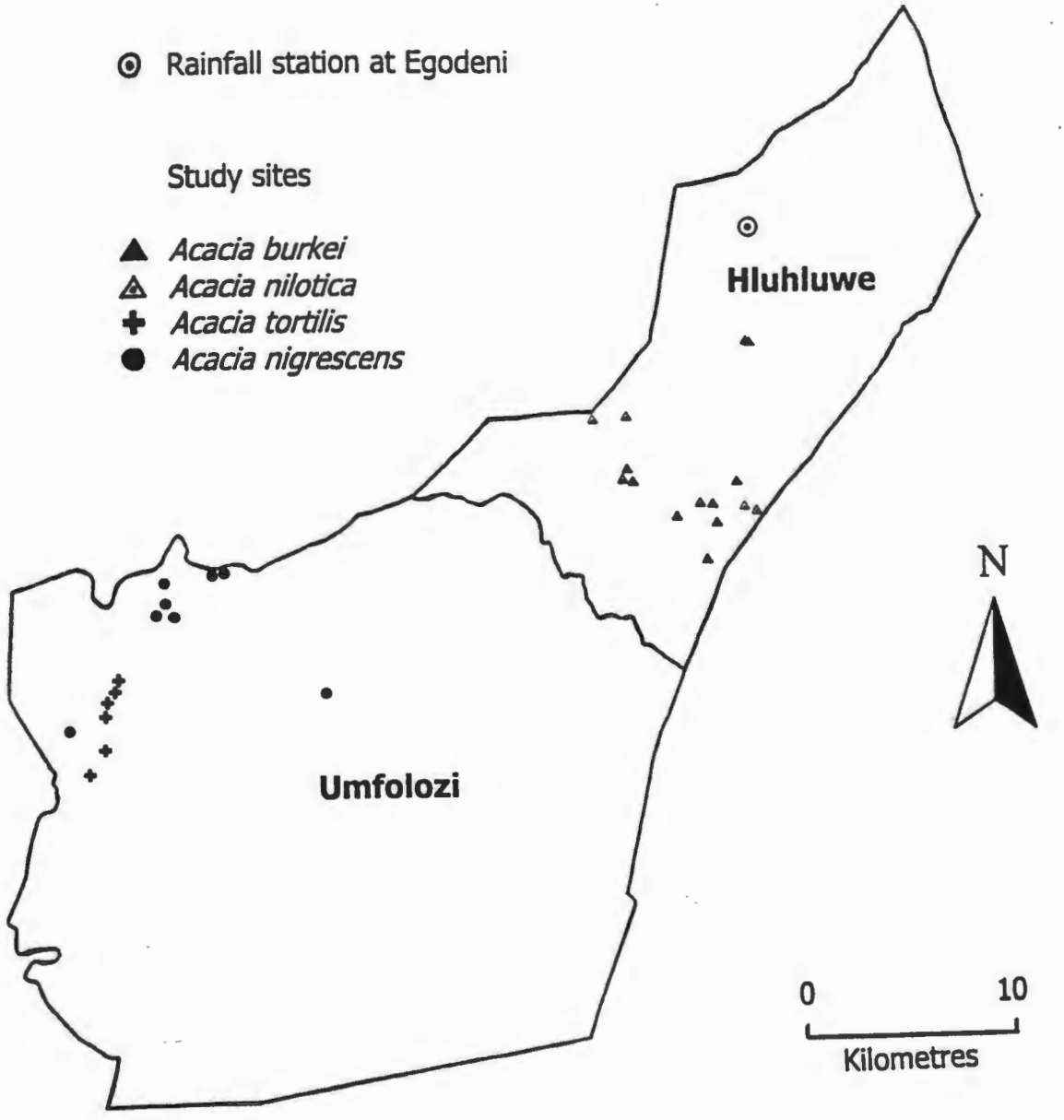

Fig 1 Map of the Hluhluwe-Umfolozi Game Reserve, showing *Acacia* stand study sites and Egodeni, where rainfall data were recorded.

Methods

Four stand-forming species of *Acacia* on the Reserve were chosen for the study. Twelve stands of *A. nilotica* and three of *A. burkei* were sampled on Hluhluwe, while eight *A. nigrescens* and six *A. tortilis* stands were sampled on Umfolozi. Adults of the species that were dominant within these stands are hereafter referred to as the stand species, while other *Acacia* species occurring among them are hereafter referred to as non-stand species.

Height size classes rather than age classes were used in the study because their height is an indication of how close these trees are to escaping fire and herbivory. In the field, five size classes were recorded but these were later condensed into three: small (0 to 0.5m), medium (0.5 to 2m), and large (taller than 2m). Many seed-producing *A. nilotica* (the shortest species at maturity of those investigated) in the study did not exceed 3m. Therefore an upper limit of 2m for the medium size class was decided upon because it appears that this species is safe from fire-induced mortality at about this height. If an upper limit of 3m, or even 2.5m had been chosen, many adults of this species would have fallen within the medium size class, indicating that they have not yet escaped the fire trap.

The Reserve road network was used to locate the study sites, all of which were within 500m of the road. Sampling was conducted within the 29 selected *Acacia* stands, most of which ranged in area from about 1ha to about 10ha. The wandering quarter transect method (Catana 1963) was used to sample stand composition. Adult *Acacia* (of any species, not necessarily the stand species) were used as markers. Beginning at a tree within the stand, the next tree chosen was the closest within a 90^0 radius in a maintained direction decided upon before commencement. Therefore although the route zigzagged, the same direction remained the bearing after each marker. This zigzag route continued until 25 marker adults were counted. The belt covered an area of five meters on either side of the line between marker adults. Within this belt, all *Acacia* (but no other genera) including the marker trees were recorded and classified according to size class.

In order to determine whether stand species were being sufficiently replaced by their own offspring over time it was necessary to compare observed abundance of *Acacia* in the study area to numbers that would be expected for a population to sustain itself. However no expected proportions for different size classes of African *Acacia* are to be found in the literature. Such information in fact seems to be lacking for savannas as a whole. In forests in different parts of the world, however, the proportion of small to medium to large tree size classes based on diameter at breast height (DBH) would convert to a ratio of 10 000 small to 100 medium to 1 large (Enquist & Niklas 2001). However, to adopt this ratio for savanna would be extremely presumptuous considering the vast differences in dynamics between the two biomes. In forests, a new recruit's main constraint is light, which is generally in short supply due to a closed or rapidly closing canopy, and competition which increases exponentially as recruits and larger individuals increase in size and shade provision (Kohyama 1991). In a savanna this competition for light is far less important. Factors such as drought and seed predation may limit recruitment (Midgley & Bond 2001). Fire is believed to present a moderate limitation to seedling survival, although it is believed, as mentioned, to have a significant effect on their progression to the medium size class (Higgins *et al.* 2000). Competition from grass, other tree species, and larger individuals of the same species for water, nutrients and space could also impose stress on smaller size classes. Similarly herbivory may force the same kind of restrictions as fire – seldom killing a small *Acacia*, but preventing or slowing it from escaping into the next size class. Considering the forest estimates as well as these limitations, it was considered conservative but safe to suggest that a ratio of three small to two medium to one large could be used as a very rough estimate of expected size class distribution for a given species of African *Acacia* in a given area. This is a very general estimate, also in view of the fact that agreement has not been reached as to whether *Acacia* establish, or are released from the fire trap in cohorts, or whether they establish and recruit steadily (Martin and Moss 1997). The former would suggest large numbers of particular size classes at a given point in time. The two-way Chi-square test (Zar 1996) was used to assess whether observed frequencies were significantly different to those predicted.

20 disc pasture meter (DPM) readings were taken at each site to provide an indication of grass density (grass biomass). All grass species that fell beneath the DPM disc at each of the 20 points were also recorded. A maximum of five grass species were found at any one DPM point, so the most prominent species was given a score of five, followed by four for the next most prominent species, and so on. By summing the scores of the species belonging to bunch or lawn grass communities for each site, a bunch grass percentage of the total was obtained.

Due to the taller height of bunch grass, it was expected that grass density measurements for sites with a high bunch grass percentage, would be higher. In order to determine whether this was the case, bunch grass percentage was compared to grass density. Densities of the small and medium size classes of stand species were compared to grass density as well as grass community type (bunch grass percentage) in order to determine whether *Acacia* recruitment is limited by, or dependent upon, the grass layer (and therefore fire). Grass density was compared to the density of large *Acacia* in order to determine whether the trees negatively affect grass density (which may in turn affect *Acacia* recruitment and therefore the future composition of stands). Densities of the large size class of stand species were also compared to densities of other size classes of the same species in order to determine whether adult density limits recruitment.

One of the longer-term projects being conducted on the Reserve was studying the recruitment and growth of trees in exclosure plots (40m x 40m). These plots were not associated with stands of *Acacia*, and this data was analysed to obtain an idea of *Acacia* demography and species composition outside of stands. Exclosure plots (EX) excluded all herbivores; control plots (CO) were unfenced, and other unfenced control plots (PA) were placed some distance from the rest of the treatments at each site to determine whether the presence of the fences affected herbivore activity. Other treatments had incomplete data and were therefore not used here. Only the numbers and species composition of *Acacia* in these plots were investigated for this study.

Soil samples were also taken at each site. Using a soil auger or pick and spade, holes were dug to a depth of just over 60cm. One sample was taken from the top 10cm and another from just below 60cm in order to detect any change in soil stratigraphy, which could indicate a change

in soil fertility or water retention. A basic analysis was performed on these samples to determine variation in soil colour, texture and structure at different sites.

Results

Size class distributions and species composition

For all *Acacia* species the predicted size class ratio against which the observed densities were compared, was three small to two medium to one large.

In *A. nilotica* stands (Fig 2), the stand species had a bimodal distribution, with few medium-sized individuals. The ratio for the stand species was 9.3 : 1 : 13.1. The other species present in significant numbers in *A. nilotica* stands was *A. karroo*. Large *A. nilotica* outnumbered large *A. karroo* by a ratio of greater than 4 : 1, but medium and small *A. karroo* outnumbered *A. nilotica*, and the overall ratio of these stands was almost three *A. karroo* to every *A. nilotica*. *A. karroo* had a "healthier" unimodal size class distribution, with a small to medium to large ratio of 15.1 : 7.8 : 1.

In *A. burkei* stands (Fig 3) large *A. burkei* that composed the stand outnumbered all other size classes and species by at least an order of magnitude. Large *A. burkei* outnumbered small *A. burkei* by a ratio of 42 : 1; small *Acacia gerrardii* by 28 : 1; and small *A. nilotica* by 16.8 : 1. Medium *A. burkei* were similarly outnumbered 28 : 1; medium *A. nilotica* 84 : 1 and medium *Acacia robusta* 42 : 1. In the few *A. burkei* stands sampled (n=3), the stand species had a strongly unimodal size class distribution, skewed towards the large size class.

In *A. tortilis* stands (Fig 4), the stand species was more numerous than any other species in all but the small size class, where there were slightly more *A. gerrardii* (1.2 : 1) than *A. tortilis*. This was largely caused by large numbers of small *A. gerrardii* at one particular site. *A. gerrardii* overall size class distribution in these stands was unimodal, with a small to medium to large ratio of 17.6 : 3.6 : 1 - a similar structure to the *A. karroo* in the *A. nilotica* stands. *A. tortilis* had a bimodal distribution with a shortage of medium-sized trees. The ratio for *A. tortilis* was 3.3 : 1 : 4.6.

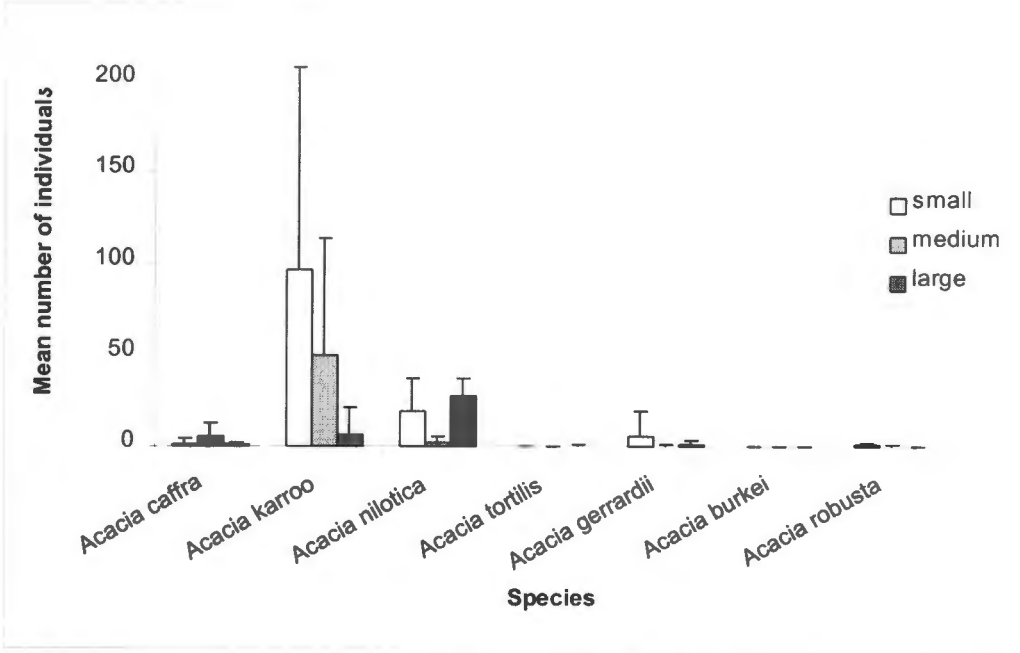

Fig 2 *Acacia* species composition and size class distribution in *Acacia nilotica* stands on Hluhluwe.

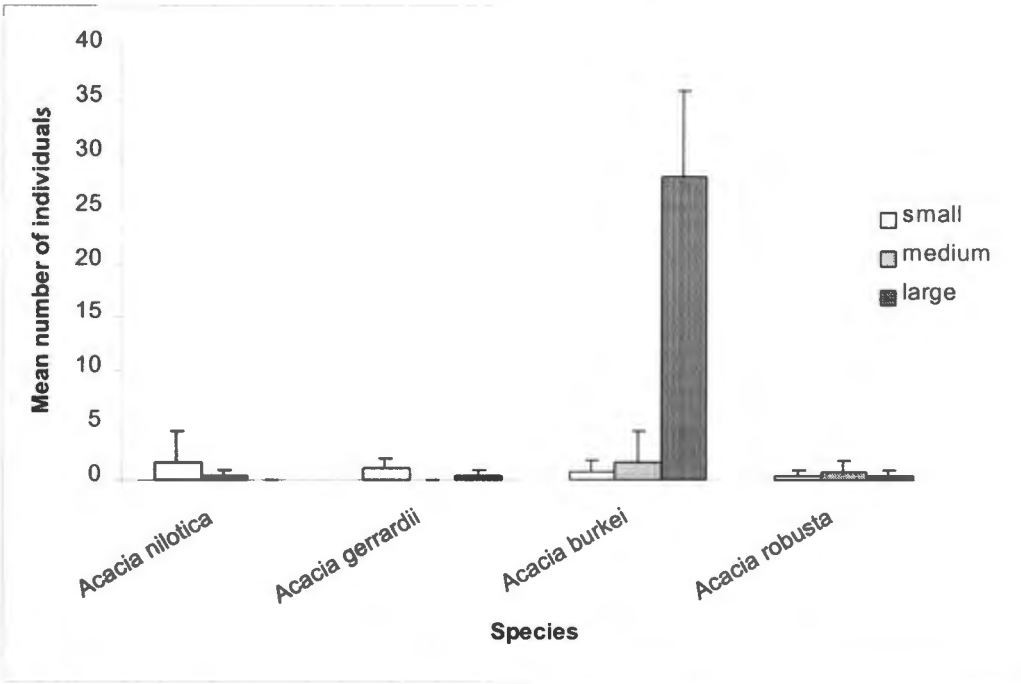

Fig 3 *Acacia* species composition and size class distribution in *Acacia burkei* stands on Hluhluwe.

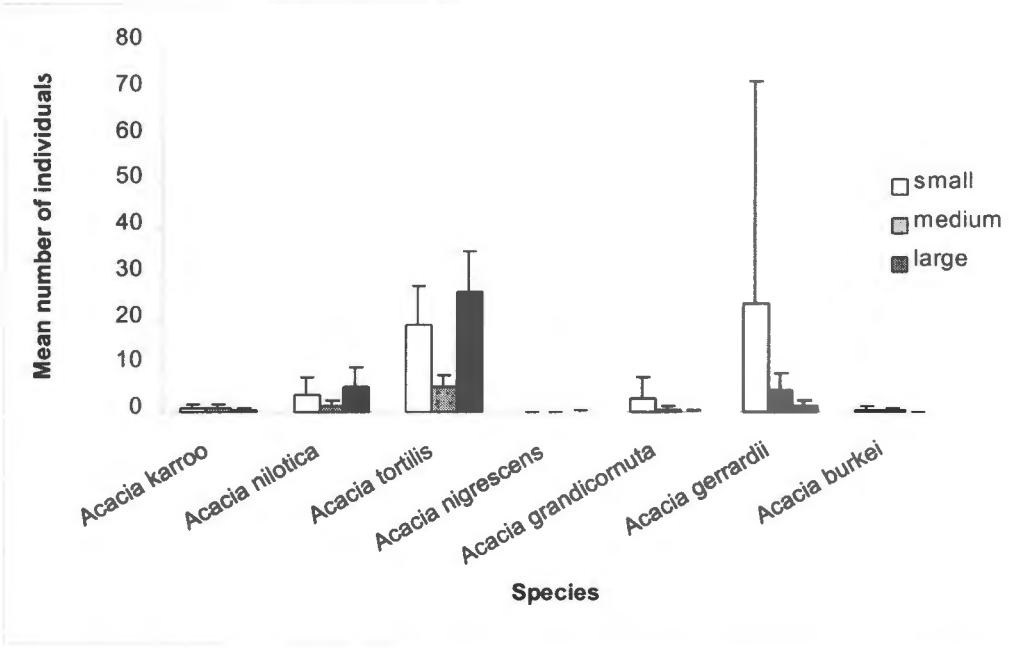

Fig 4 *Acacia* species composition and size class distribution in *Acacia tortilis* stands on Umfolozi.

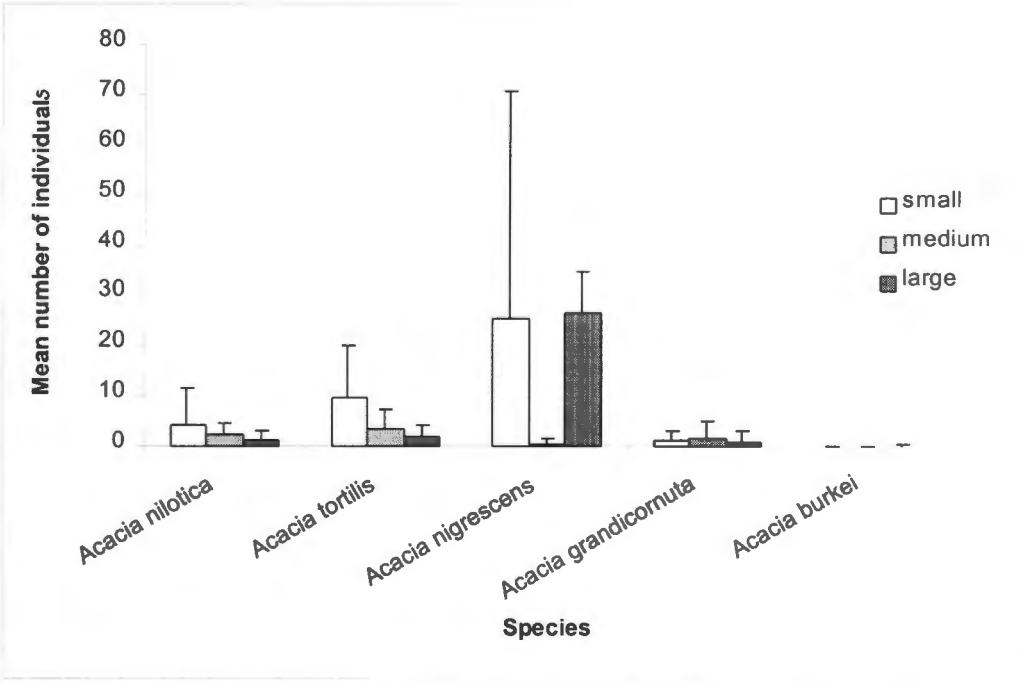

Fig 5 *Acacia* species composition and size class distribution in *Acacia nigrescens* stands on Umfolozi

In *A. nigrescens* stands (Fig 5), the same bimodal size class structure was found as for *A. nilotica* and *A. tortilis*, but even more pronounced. Three other *Acacia* species, although all with fewer large, small and overall individuals than *A. nigrescens*, had more medium-sized trees than the stand species. These were, *A.tortilis*, *A. nilotica* and *Acacia grandicornuta*. The species with second and third most trees overall (*A. tortilis* and *A. nilotica* respectively), had unimodal size class distributions with small outnumbering medium and medium outnumbering large. The bimodal distribution of *A. nigrescens* however represented a ratio of 51 : 1 : 53.5.

Observed numbers of *A. nilotica*, *A. burkei*, *A. nigrescens* and *A. tortilis* in their respective stands, were all found to be significantly different to their respective predicted frequencies of one large to two medium to three small ($p < 0.001$ in all cases) using the two-way Chi-square test (Zar 1996). In all cases ($p < 0.001$) the observed number of large far exceeded that of medium. Except in the case of *A. burkei*, the small also far outnumbered the medium ($p < 0.001$). In the case of *A. burkei*, the medium to small ratio was as expected ($0.01 < p < 0.05$). In all four species large significantly outnumbered small individuals ($p < 0.001$), particularly in the case of *A. burkei*.

The most abundant non-stand species for each stand were also analysed, with the exception of *A. burkei* stands, where none was abundant enough to merit doing so. In *A. nilotica* stands this species was *A. karroo*; in *A. nigrescens* stands, *A. tortilis*; and in *A. tortilis* stands, *A. gerrardii*. In all three cases, these species had a unimodal size class distribution that was skewed primarily towards the small size class, and secondarily towards the medium size class. In all cases the small to medium and medium to large ratios were greater than expected ($p < 0.001$). These ratios lend support to the expected ratios postulated in this study as a conservative expectation for *Acacia* in general on the Reserve, which fall between the bimodal stand species size class distribution and the unimodal distribution of the non-stand species.

Tables of values for Fig 2 to Fig 5 are attached in Appendix 1.

Correlations with size class distribution and species composition

Grass

A number of relationships were tested between grass density and numbers of individuals in different *Acacia* size classes and species to determine whether *Acacia* recruitment is correlated with grass density (Tables 1 to 5). These relationships were tested for particular *Acacia* species within each stand, for combined *Acacia* species in each stand, and for combined *Acacia* species in all 29 sites together. None were however significant at the 95% interval, with the exception of a positive relationship between grass density and numbers of small *A. nilotica* in *A. nigrescens* stands ($n = 8$, $r^2 = 0.717$, $0.005 < p < 0.025$) (Fig 6). The strength of this regression was however largely affected by a single datum (160.5; 79.1), without which the relationship would not have been significant.

A comparison of percentage bunch grass with grass density for each site and combined sites produced no significant relationships. Bunch grass percentage was plotted against the same sets of data as grass density to test whether the community type was a better indicator of potential fuel load than the standing grass biomass after the growing season. Again, however, no relationships emerged, with the single exception of a weak but significant ($n = 6$, $r^2 = 0.7753$, $0.01 < p < 0.05$) positive relationship between bunch grass and *A. nilotica* seedlings in *A. tortilis* stands (Fig 7).

Adult density

No significant relationships were found between large *Acacia* densities and the densities of smaller *Acacia*. The only exception to this was obtained when comparing the log of small density with the log of large density for all sites combined (Fig 8). This produced a weak positive but significant relationship at the 95% interval ($n = 29$, $r^2 = 0.233$, $p = 0.0124$). When comparing the density of large *Acacia* with grass density and grass community type no significant relationships were found.

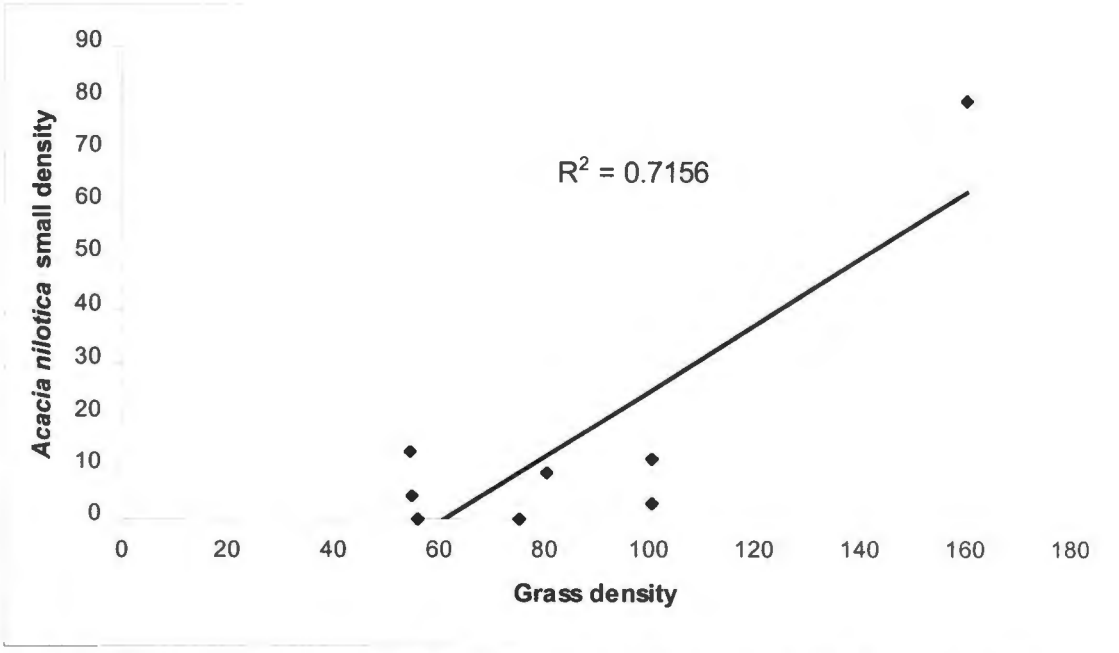

Fig 6 The relationship between the density of small *A. nilotica* individuals and grass density at *A. nigrescens* sites. Note influence of outlier on overall regression.

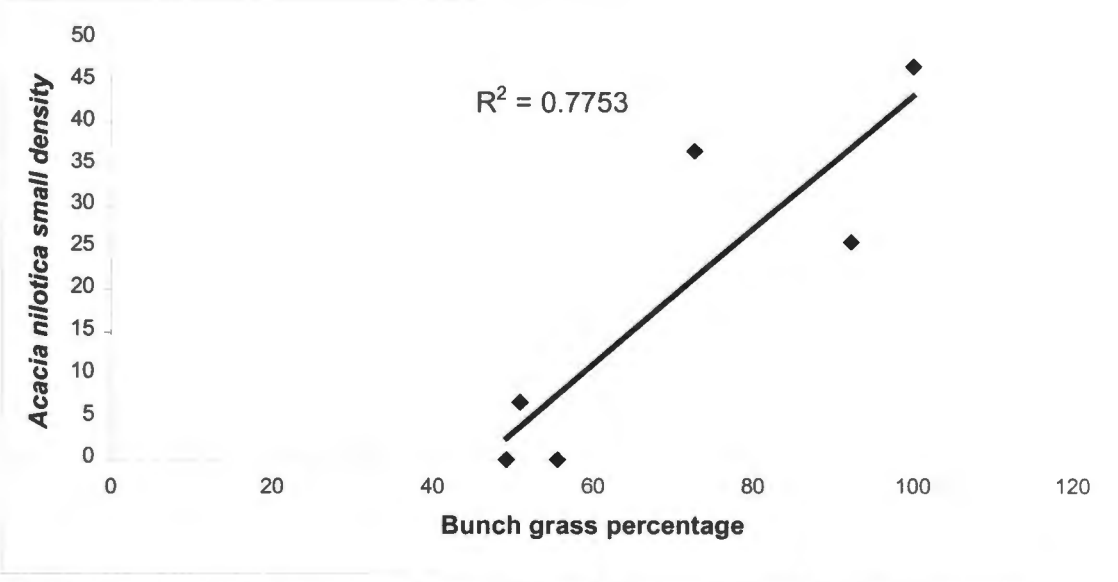

Fig 7 The relationship between the density of small *A. nilotica* individuals and percentage bunch grass at *A. tortilis* sites.

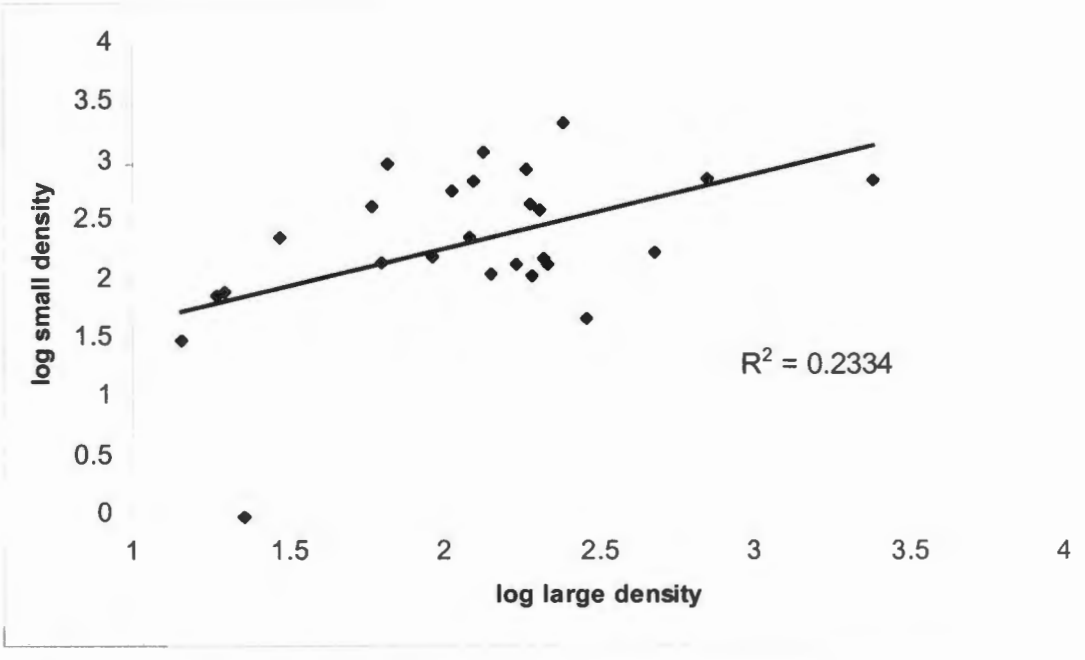

Fig 8 The relationship between the log of density of total small individuals and the log of density of total large individuals at all 29 sites combined.

Table 1 Results of regression analyses for *A. nilotica* stands. Significance was tested at the 95% interval for all relationships. Blank cells mean that no analysis was conducted. N/S = not significant at the 95% interval. TOT S DNS = total small density; TOT M DNS = total medium density; TOT L DNS = total large density; GRS DNS = grass density; BUNCH = bunch grass percentage; AN S DNS = *A. nilotica* small density; AK S DNS = *A. karroo* small density; AN M DNS = *A. nilotica* medium density; AK M DNS = *A. karroo* medium density.

	TOT S DNS	TOT M DNS	TOT L DNS	GRS DNS	BUNCH	AN S DNS	AK S DNS	AN M DNS	AK M DNS
TOT S DNS			N/S	N/S	N/S				
TOT M DNS				N/S					
TOT L DNS	N/S			N/S	N/S		N/S		
GRS DNS	N/S	N/S	N/S		N/S	N/S	N/S	N/S	N/S
BUNCH	N/S		N/S	N/S		N/S	N/S		
AN S DNS				N/S					
AK S DNS			N/S	N/S					
AN M DNS				N/S	N/S				
AK M DNS				N/S	N/S				

Table 2 Results of regression analyses for *A. burkei* stands. Significance was tested at the 95% interval for all relationships. N/S = not significant at the 95% interval. TOT S DNS = total small density; TOT M DNS = total medium density; TOT L DNS = total large density; GRS DNS = grass density; BUNCH = bunch grass percentage; AB S DNS = *A. burkei* small density.

	TOT S DNS	TOT M DNS	TOT L DNS	GRS DNS	BUNCH	AB S DNS
TOT S DNS			N/S	N/S		
TOT M DNS				N/S		
TOT L DNS	N/S			N/S		
GRS DNS	N/S	N/S	N/S		N/S	N/S
BUNCH				N/S		
AB S DNS				N/S		

Table 3 Results of regression analyses for *A. tortilis* stands. Significance was tested at the 95% interval for all relationships. Blank cells mean that no analysis was conducted. N/S = not significant at the 95% interval. TOT S DNS = total small density; TOT M DNS = total medium density; TOT L DNS = total large density; GRS DNS = grass density; BUNCH = bunch grass percentage; AT S DNS = *A. tortilis* small density; AG S DNS = *A. gerrardii* small density; AN S DNS = *A. nilotica* small density.

	TOT S DNS	TOT M DNS	TOT L DNS	GRS DNS	BUNCH	AT S DNS	AG S DNS	AN S DNS
TOT S DNS			N/S	N/S	N/S			
TOT M DNS				N/S	N/S			
TOT L DNS	N/S			N/S		N/S		
GRS DNS	N/S	N/S			N/S	N/S	N/S	N/S
BUNCH	N/S	N/S	N/S	N/S		N/S	N/S	$R^2 = 0.775$
AT S DNS			N/S	N/S	N/S			
AG S DNS				N/S	N/S			
AN S DNS				N/S	$R^2 = 0.775$			

Table 4 Results of regression analyses for *A. nigrescens* stands. Significance was tested at the 95% interval for all relationships. Blank cells mean that no analysis was conducted. N/S = not significant at the 95% interval. TOT S DNS = total small density; TOT M DNS = total medium density; TOT L DNS = total large density; GRS DNS = grass density; BUNCH = bunch grass percentage; NG S DNS = *A. nigrescens* small density; AT S DNS = *A. tortilis* small density; AN S DNS = *A. nilotica* small density.

	TOT S DNS	TOT M DNS	TOT L DNS	GRS DNS	BUNCH	NG S DNS	AT S DNS	AN S DNS
TOT S DNS			N/S	N/S	N/S			
TOT M DNS				N/S	N/S			
TOT L DNS	N/S			N/S		N/S		
GRS DNS	N/S	N/S			N/S	N/S	N/S	$R^2 = 0.717$
BUNCH	N/S	N/S	N/S	N/S		N/S	N/S	N/S
NG S DNS			N/S	N/S	N/S			
AT S DNS				N/S	N/S			
AN S DNS				$R^2 = 0.717$	N/S			

Table 5 Results of regression analyses for all stands combined. Significance was tested at the 95% interval for all relationships. Blank cells mean that no analysis was conducted. N/S = not significant at the 95% interval. TOT S DNS = total small density; TOT M DNS = total medium density; TOT L DNS = total large density; GRS DNS = grass density; BUNCH = bunch grass percentage; LOG L DNS = log of large density; LOG S DNS = log of small density.

	TOT S DNS	TOT M DNS	TOT L DNS	GRS DNS	BUNCH	LOG L DNS	LOG S DNS
TOT S DNS				N/S	N/S		
TOT M DNS				N/S			
TOT L DNS	N/S			N/S	N/S		
GRS DNS	N/S	N/S	N/S		N/S		
BUNCH	N/S		N/S	N/S			
LOG L DNS							$R^2 = 0.233$
LOG S DNS						$R^2 = 0.233$	

Plot data

Data from exclosure plots (EX) (Fig 9) showed no noticeable difference in size class distribution to control plots (CO and PA) (Fig 10 & 11) for *A. nilotica*, *A. nigrescens* and *A. tortilis*. In all the treatments *A. nigrescens* had either a bimodal size class distribution, or slightly more large than medium individuals – in both cases there were many more small than either large or medium. *A. nilotica* had slightly more large than medium in PA plots, and a unimodal distribution in CO and EX plots. *A. tortilis* had unimodal distribution for EX, PA and CO plots. In all cases in these plots the unimodality of the data refers to more small than medium, and more medium than large.

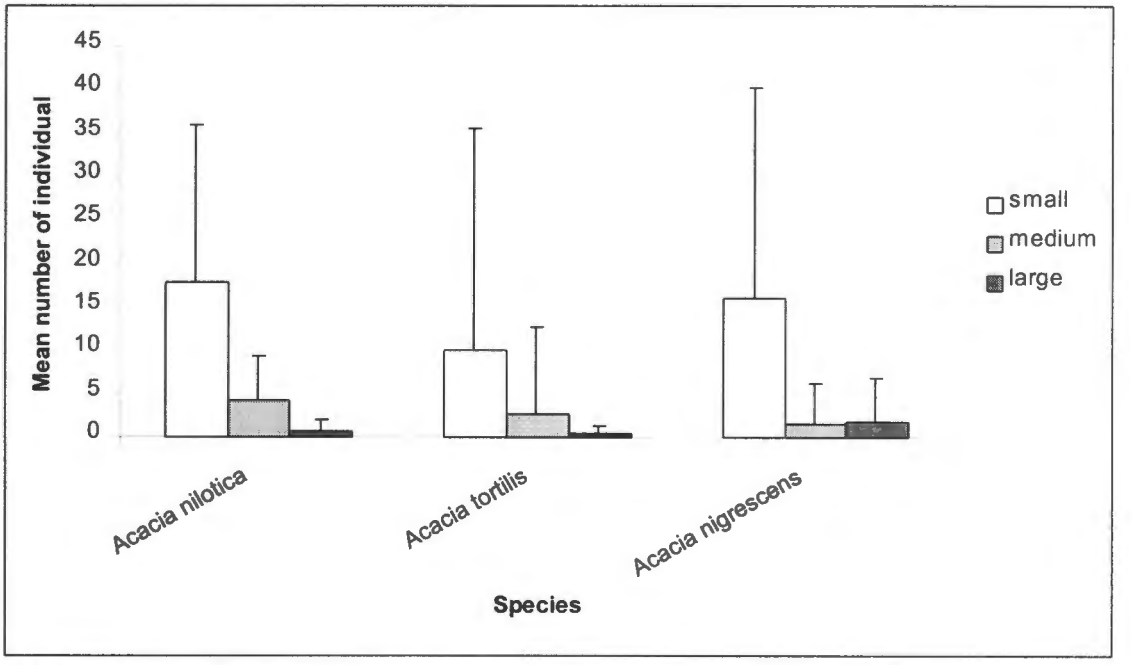

Fig 9 *Acacia* species composition and size class distribution in exclosure (EX) plots.

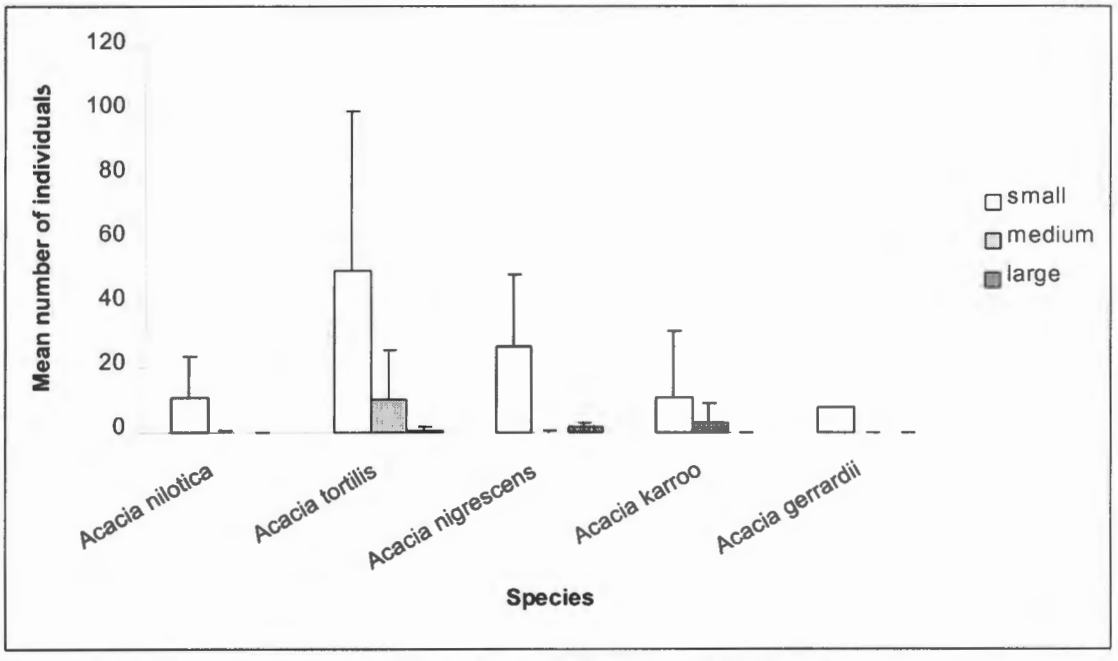

Fig 10 *Acacia* species composition and size class distribution in control (CO) plots.

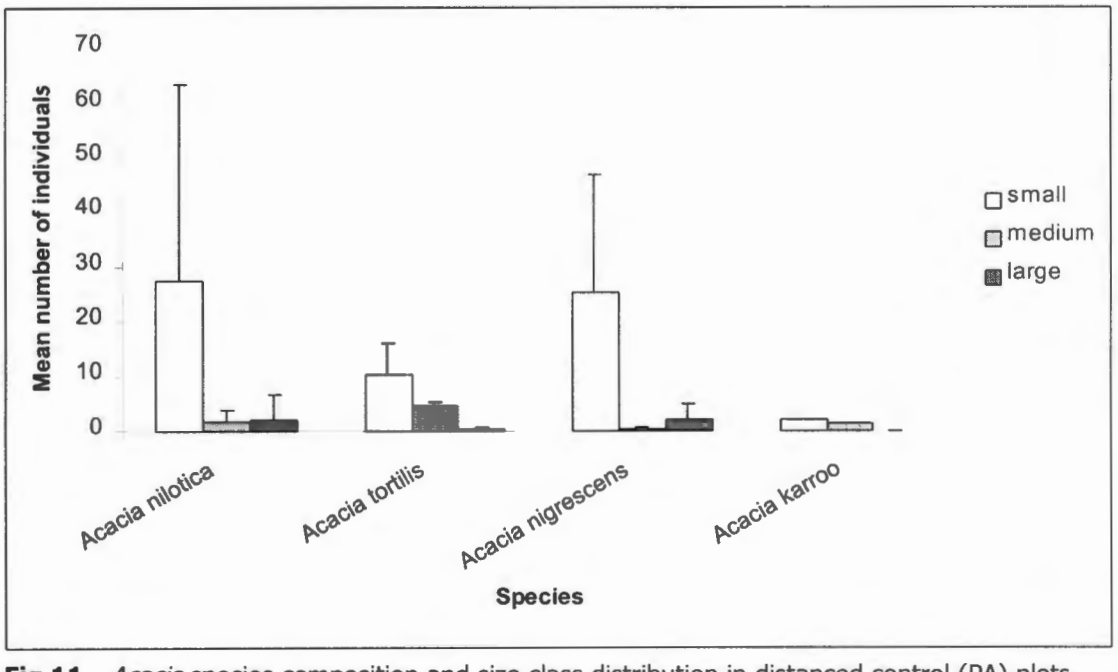

Fig 11 *Acacia* species composition and size class distribution in distanced control (PA) plots.

Soil

No duplex soils were discovered at the study sites. There was little variety between the soils of sites of different stand species with the exception of the *A. burkei* stands. While the other stands had dark sandy clays with occasional gritty clay, gravelly clay and sandy clay loam, the *A. burkei* stands all grew in lighter-coloured, apedal sand. This sand was in all three cases slightly water-repellent.

Discussion and conclusions

Bond and co-workers (2001) found that the composition of *A. nilotica* stands on Hluhluwe was in a state of change. In investigating *A. nilotica* stands and stands of other species, this study confirmed those findings, and suggests that stands of other *Acacia* species on the Reserve may be approaching such a situation. The study attempted to establish reasons for differences in size class structure of stand and non-stand species by investigating relationships between soil, densities of different *Acacia* species and size classes, and grass layer density and composition, but with no conclusive results.

Had it been found that different *Acacia* species were unique to different soil types, it would suggest that edaphic conditions are the major determinant of their distribution. The lack of distinction between soils of different species' stands, however, indicates that soil is not a determining factor in the species composition of *Acacia* stands. The one exception was the case of *A. burkei*, which, as supported by this study, has been found to prefer sandy soils (Pooley 1993, Coates Palgrave 2002). The slight water repellence of these soils has not been noted before. Its significance has not been investigated, but together with the sandy structure of the soil may mean that these soils are more prone to desiccation and nutrient leaching (Miller & Donahue 1990), which could prevent other *Acacia* species from utilizing these sites.

Stand species' size class distribution suggests that fire and recruitment are both limiting factors in the stand species of *Acacia* investigated. Very few individuals of medium height were found, and it can be argued that the resultant bimodality of size class distribution is to be

expected in fire-prone systems like these savannas, where small individuals may be suppressed for some time before conditions allow their escape from the fire trap (Higgins *et al.* 2000). However, both non-stand *Acacia* species in stands and those from plots not associated with stands, generally did not display this bimodal size class distribution. This despite the fact that two of these species, *A. nilotica* and *A. tortilis*, had bimodally distributed size classes as stand species. Also, aside from the extreme shortage of medium individuals, the peaks of the bimodal distribution of stand species were skewed towards the large size class, whereas one would expect more small individuals (seedlings as well as gullivers) than large.

The overall trend is that the stand species are not being replaced at the rate expected. Despite the slight positive influence that the presence of adults appears to have on the number of smaller *Acacia* present (Fig 8), the numbers of small individuals of stand species compared with small individuals of non-stand species suggests that conditions favour certain species independently of the quantity and proximity of parent trees.

This study was conducted after the growing season of a drier than usual year on the Reserve. Disc pasture meter readings were lower than expected, and this may have been due to the senescence and resultant brittleness of the grass. It may be for this reason that no correlates were found between the density of grass or grass community type, and the various *Acacia* size classes. Bunch grass percentage was, however, also compared to the *Acacia* densities, with only one weak relationship emerging. This leaves the possibility that these *Acacia* species are too dissimilar to lump together to test such relationships, and the likelihood that individual sample sizes were too small to detect patterns. Indeed it has been stated that there is an enormous variation between and within *Acacia* species, which may depend on area, habitat and time (Gourlay 1995, Midgley & Bond 2001). It may be that more useful information would have been gleaned with the same time available, if only one species had been investigated. The drawback would be, however, that the data, although of higher resolution, would tell us nothing about any other *Acacia* species.

Scholes and Archer (1997) noted that savanna trees' effect on grass can range from positive to neutral to negative, depending on factors such as ecophysiological characteristics of both tree and grass, availability of resources, extent of herbivory/granivory, and disturbances like fire. Although possibly too scant to make any bold statements, the data collected in this study did not produce signs of any patterns, suggesting that these *Acacia* species are neither dependent on grass density (and therefore fire intensity and frequency), nor is the small size class dependent on the density or sparseness of adults.

An observation in grass-denuded *A. nigrescens* stands may merit further investigation in future: In grass-denuded areas, most small *A. nigrescens* grew amongst the protective branches of adults. In some cases these branches had been broken off by elephant and in others they belonged to adults that had been pushed over. In these denuded patches fire is suppressed by the lack of a fuel load; herbivory is prevented by the formidable cages of thorny dry branches; and the adult tree has pumped nutrients to the area (Scholes & Archer 1997). This combination of factors seems favourable for the recruitment of seedlings, particularly with a potential source of seed directly in situ. The surrounding matrix of denuded ground may be a requirement for establishment if fire is a severely limiting factor. If these sites are particularly favourable for their growth, it is possible that *A. nigrescens* seedling recruitment is dependent on the senescence of adults in order to provide the protection if not the space they require for their establishment. *A. nigrescens* was the only species discussed in this study, that had less medium than large or small individuals in every instance that it was encountered, which may suggest that at the time these trees were at a stage where a number of adults were becoming senescent and "giving way" to a new generation.

Only the *A. nilotica* seedlings in the *A. nigrescens* stands produced a positive correlation with grass density and only the *A. nilotica* seedlings in the *A. tortilis* stands produced a positive correlation with bunch grass percentage. This could suggest that this species is more fire-adapted than previously believed. However, these stands were on the less fire-prone Umfolozi, where *A. nilotica* is currently far less abundant than on Hluhluwe. It is on Hluhluwe where *A.*

nilotica stands appear to be giving way to *A. karroo*. The question may be asked whether the former species is in the process of migrating to an area where the combination of fire and competition with a vigorous, fire-tolerant species (*A. karroo*) is less of a threat.

Clearly there is much still to learn about the population dynamics of the African *Acacia*, and what will become of stands such as those investigated in this study. Prior to 1983 *A. karroo* was largely confined to river valleys on the Reserve (Whately & Porter 1983), and now it is widely found on Hluhluwe. It thus appears that already considerable change has occurred. I believe that individual species' life histories are too different to study in combination, and that separate, similar studies on separate species are worth the extra time involved. In a system subject to management that attempts to mimic nature as accurately as possible for the greater good of the its components, detailed information is essential, and is appropriate considering the astounding complexity of this biome.

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Appendix 1

Table I Species composition and size class distribution in *Acacia nilotica* stands

	small	medium	large	dead	TOTAL
Acacia caffra	1	60		0	**84**
Acacia karroo	1162	603	7	4	**1846**
Acacia nilotica	23	25	32	10	**691**
Acacia tortilis	0	0		0	**2**
Acacia nigrescens	0	0		0	**0**
Acacia grandicornuta	0	0		0	**0**
Acacia gerrardii	6	4	1	1	**77**
Acacia burkei	1	0		0	**2**
Acacia robusta	8	2		0	**10**
TOTAL	**148**	**694**	**42**	**111**	**2712**

Table II Species composition and size class distribution in *Acacia burkei* stands

	small	medium	large	dead	TOTAL
Acacia caffra	0	0		0	**0**
Acacia karroo	0	0		0	**0**
Acacia nilotica	5	1		0	**6**
Acacia tortilis	0	0		0	**0**
Acacia nigrescens	0	0		0	**0**
Acacia grandicornuta	0	0		0	**0**
Acacia gerrardii	3	0		0	**4**
Acacia burkei	2	5	8	6	**97**
Acacia robusta	1	2		0	**4**
TOTAL	**1**	**8**	**8**	**6**	**111**

Table III Species composition and size class distribution in *Acacia tortilis* stands

	small	medium	large	dead	TOTAL
Acacia caffra	0	0		0	**0**
Acacia karroo	6	4		0	**13**
Acacia nilotica	2	7	3	14	**77**
Acacia tortilis	11	34	15	8	**311**
Acacia nigrescens	0	0		0	**1**
Acacia grandicornuta	1	2		0	**21**
Acacia gerrardii	14	29		0	**178**
Acacia burkei	2	2		0	**4**
Acacia robusta	0	0		0	**0**
TOTAL	**30**	**7**	**20**	**2**	**605**

Table IV Species composition and size class distribution in *Acacia nigrescens* stands

	small	medium	large	dead	TOTAL
Acacia caffra	0	0		0	**0**
Acacia karroo	0	0		0	**0**
Acacia nilotica	3	18		1	**61**
Acacia tortilis	7	28	1	1	**122**
Acacia nigrescens	20	4	21	17	**439**
Acacia grandicornuta	9	13		0	**29**
Acacia gerrardii	0	0		0	**0**
Acacia burkei	0	0		0	**1**
Acacia robusta	0	0		0	**0**
TOTAL	**32**	**6**	**24**	**1**	**652**

Appendix 2

Table I Species composition and size class distribution in exclosure (EX) plots. Mean values given.

	small	medium	large	TOTAL
Acacia nilotica	17.85714	4.285714	0.571429	**22.7143**
Acacia tortilis	10.14286	2.714286	0.428571	**13.2857**
Acacia nigrescens	16.14286	1.571429	1.714286	**19.4286**
TOTAL	**44.1429**	**8.57143**	**2.71429**	**55.4286**

Table II Species composition and size class distribution in control (CO) plots. Mean values given.

	small	medium	large	TOTAL
Acacia nilotica	1	0.25	0	**11.2**
Acacia tortilis	50.2	10.5	0.75	**61.5**
Acacia nigrescens	26.7	0.25	2	**2**
Acacia karroo	10.7	2.75	0	**13.5**
Acacia gerrardii	7.75	0	0	**7.75**
TOTAL	**95.5**	**13.5**	**2.75**	**111.7**

Table III Species composition and size class distribution in distanced control (PA) plots. Mean values given.

	small	medium	large	TOTAL
Acacia nilotica	27.5	1.75	2.25	**31.**
Acacia tortilis	10.2	4.5	0.25	**1**
Acacia nigrescens	25.2	0.25	2.25	**27.7**
Acacia karroo	2.25	1.25	0	**3.**
TOTAL	**65.2**	**7.75**	**4.75**	**77.7**